RHODORA, Vol. 91, No. 866, pp. 172–187, 1989

MORPHOLOGICAL VARIATION IN SOUTHERN APPALACHIAN *BETULA ALLEGHANIENSIS* AND *B. LENTA* (BETULACEAE)

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ABSTRACT

Variation in leaf, fruit, bract, and catkin morphology of *Betula alleghaniensis* Britt. and *B. lenta* L. was studied along the elevational gradient in the southern Appalachians in order to characterize the regional structure of the two species. Populations at 52 sites were sampled in North Carolina and adjacent parts of Tennessee, Georgia, and South Carolina. Weak to moderate linear relationships with elevation were found in most size attributes for both species. A few shape characters were also correlated with elevation for one or the other species. *Betula alleghaniensis* was significantly more variable than *B. lenta* for 28 of the 44 characters analyzed. Levels of variability in both species approximated or exceeded levels found in other regions. Low-elevation rather than high-elevation southern Appalachian *B. alleghaniensis* appears to be more similar to the northern form. However, due to the nature of the morphological cline, the authors found no validity to varietal distinctions in yellow birch.

Key Words: *Betula,* birch, cline, morphology, phenotypic variation, southern Appalachians

INTRODUCTION

Both *Betula alleghaniensis* Britt. (yellow birch) and *B. lenta* L. (sweet, black, or cherry birch) belong to Winkler's (1904) subsection *Costatae* Regel of Section *Eubetula* Regel. This subsection, with its center of diversity in northeastern Asia, includes only four taxa native to North America: *B. alleghaniensis, B. lenta, B. nigra* L. (river birch), and *B. uber* (Ashe) Fern. (round-leaf birch). Morphological, chemical, and hybridization data indicate a close affinity between yellow and sweet birch. The rare round-leaf birch is thought to be allied to sweet birch (Sharik and Ford, 1984). River birch is considered distantly related to sweet and yellow birch (Clausen, 1973).

Both yellow and sweet birch are important, widespread hardwood components of the Appalachian forests. Sweet birch is found from Maine south to the mountains of Alabama and Georgia

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(Little, 1971). Yellow birch ranges from Ontario east to Nova Scotia and south to the mountains of Georgia and South Carolina (Little, 1971; Clausen, 1973).

The elevational amplitude of both species is greatest in the southern Appalachians. Here, yellow birch ranges in elevation from 300 m to 1900 m, and sweet birch from 300 m to 1550 m. The two occur together at mid-elevations (600 m to 1400 m) in association with other components of the mixed mesophytic forest. In this area of sympatry, yellow birch and sweet birch occur intermixed on moister slopes. On drier slopes, yellow birch grows most often along streamsides; sweet birch is typically found further upslope.

Morphological variation in both taxa, particularly in yellow birch, has been the source of some confusion over the years, as evidenced by the nomenclature which has entered into the literature and its subsequent application. Britton (1904) wrote of his newly segregated yellow birch, *Betula alleghaniensis,* that it resembled both *B. lutea* Michx. f. (then the standard name for yellow birch; now a synonym of *B. alleghaniensis*) and *B. lenta,* though it was smaller than *B. lutea.* Britton further described his new taxon as having bark "either close and furrowed, or peeling off in thin yellowish-gray layers," and leaves "mostly cordate at the base but sometimes rounded." The type specimen for this new yellow birch was collected on the upper slopes of Mt. Pisgah in western North Carolina, though he stated that it ranges to Quebec and northern Michigan. Britton (1908) further distinguished the two yellow birches on the basis of fruiting scale length. *Betula alleghaniensis* had short bracts, only 4 to 6 mm long, compared to bracts 8 to 10 mm long for *B. lutea.*

Blanchard (1911) drew attention to another yellow birch variant, a dark, tight-barked form, which he asserted had been confused with sweet birch in the north, northeast, and northwest. Fassett (1932) described the dark, tight-barked form as *Betula lutea* forma *fallax* and commented that such individuals perhaps form the basis of reports of sweet birch from Wisconsin. In their studies in Michigan, Dancik (1969) and Dancik and Barnes (1971) found that degree of exfoliation and bark color were not correlated with size and age. They attributed the variation to genetic differences among trees and concluded that the form was not worthy of any higher taxonomic status.

Whittaker (1956) found that both yellow birch and sweet birch were apparently bimodally distributed along the elevational gradient in the Great Smoky Mountains. Both species also showed evidence of altitudinal differentiation. Whittaker suggested that the low-elevation yellow birch was *Betula alleghaniensis,* and the high-elevation yellow birch was *B. lutea,* the one found at more northerly latitudes.

Subsequent studies of range-wide or regional variation in natural stands of yellow birch have demonstrated significant differences over the range of the species in catkin, fruit, and bract characteristics, but no obvious geographic trends. Dancik and Barnes (1975) found significant differences in the variability of leaf characters among populations in the upper Great Lakes region. They also found that populations with a similar complex of site conditions shared similar leaf morphology. In a subsequent study of regional morphological variation, Sharik and Barnes (1979) sampled twenty-nine populations of yellow birch over five elevational transects from North Carolina to Vermont. They found significant differences among populations in leaf, catkin, bract, fruit, pollen, and bark attributes. Approximately 30% of the characters included in that study showed consistent trends with latitude or elevation.

Sharik and Barnes (1979) also reported regional variation in sweet birch in the Appalachians. Results were similar to those for yellow birch. There were significant differences between populations. More characters were significantly correlated with latitude in this species than in *Betula alleghaniensis,* although fewer (less than 20%) were correlated with elevation.

Although there is evidence of population differentiation in both species, few consistent geographic or environmental trends have been demonstrated. The broad geographic scope of the work discussed above and the extent of variation found over the ranges of the taxa may have concealed any trends that developed in response to environmental gradients. Because at least two investigators have asserted that two yellow birch taxa are present (and Whittaker equally strongly that there are two sweet birch ecotypes) in the southern Appalachians, it was concluded that a study based on intensive sampling in this relatively restricted area was needed to assess the nature and patterning of variation in both species. Specifically, the purpose of this study was to determine if the two species vary in a consistent fashion in their leaf, fruit, bract, or catkin morphology with elevation in the southern

Appalachians. The quantification of any discernible relationships with elevation and the comparison of patterns of variation in the two species over the elevation gradient was also of interest. Finally, if systematic patterns of variation do exist, are they sufficient to justify specific, subspecific, or varietal distinctions in either or both *Betula alleghaniensis* and *B. lenta*?

METHODS

During the summer of 1979, populations of sweet birch and yellow birch were sampled at 52 different sites in North Carolina and adjacent parts of Tennessee, Georgia, and South Carolina (Table 1). Female catkins were collected from 134 of the 208 sweet birches sampled and 113 of the 310 yellow birches sampled. Sweet birch was sampled from 460 m to 1500 m, and yellow birch from 460 m to 1900 m. Yellow birch was sampled at 36 of the 52 sites, and sweet birch at 34 of the 52 sites.

Catkins were collected with pole pruners and measured before the samples were pressed and dried. All other measurements were made from pressed specimens. A list of characters measured and ratios derived from them is available from the senior author upon request. Most length measurements are as defined in Sharik and Barnes (1971). In addition to the 27 characters measured, 17 new variables were generated as ratios of the original characters.

Individual tree averages consisted of measurements from five leaves, usually one from each of five spur shoots, and five bracts and samaras taken from the central portion of one catkin. For catkin length and width, five catkins were usually measured, although for a few trees from one to four catkins were used. Gland concentration was the average number seen whole in ten fields of view at 100 × magnification. Average stomate concentration was determined from ten fields of view at 450 × magnification. Guard cell length was an average of five measurements taken between the third and fourth secondary vein of one leaf.

All statistical analyses were performed by computer programs in the SAS package (SAS Institute Inc., 1985a, 1985b). Summary statistics for each population, species means averaged across populations, and correlation coefficients of yellow and sweet birch morphological characters with elevation are available from the senior author upon request.

Voucher specimens are deposited at NCU.

Table 1. Population descriptions and number of trees sampled at each site for *Betula alleghaniensis* (yellow birch) and *B. lenta* (sweet birch). Numbers in parentheses are the number of fertile trees sampled out of the total number sampled to the left. The Blue Ridge Parkway is abbreviated BRP.

					Sample Size	
No.	Pop.	County, State	Site Description	Elev. (m)	Yellow Birch	Sweet Birch
1	6	Rabun, GA	0.7 mi. from GA/NC border on GA 28	700	–	5 (5)
2	7	Rabun, GA	4.0 mi. from GA/SC border on GA 28	670	–	5 (4)
3	14	Rabun, GA	Tallulah R. just off US 23/441	520	–	5 (0)
4	28	Rabun, GA	Betty Cr. Rd. off US 23/441	700	–	5 (5)
5	48	Towns, GA	Brasstown Bald	1430	16 (4)	–
6	49	Towns, GA	Brasstown Bald	1130	–	5 (5)
7	38	Buncombe, NC	Milepost 394 on BRP	670	–	5 (5)
8	57	Buncombe, NC	W slope of Craggy Dome	1740	5 (3)	–
9	35	Caldwell, NC	Watauga/Caldwell Co. line on US 221	1220	29 (5)	5 (5)
10	9	Clay, NC	Standing Indian Mtn.	1650	10 (0)	–
11	10	Clay, NC	Standing Indian Mtn.	1550	9 (0)	–
12	11	Clay, NC	Standing Indian Mtn.	1490	10 (0)	5 (0)
13	13	Clay, NC	Standing Indian Mtn.	1400	10 (0)	–
14	45	Clay, NC	Forest Service Rd. 71 just off US 64	1100	21 (17)	11 (11)
15	16	Haywood, NC	Richland Balsam Mtn.	1890	4 (0)	–
16	17	Haywood, NC	Bear Pen Gap on BRP	1710	5 (0)	–
17	23	Haywood, NC	Balsam Gap Overlook on BRP	1100	29 (0)	5 (0)
18	25	Haywood, NC	Waterrock Knob	1800	5 (1)	–
19	26	Haywood, NC	Waterrock Knob	1890	5 (0)	–
20	53	Haywood, NC	View of John Rock on BRP	1620	5 (4)	–
21	37	Henderson, NC	Henderson/Transylvania Co. line on NC 280	670	–	5 (4)
22	20	Jackson, NC	0.7 mi. from Macon/ Jackson Co. line on US 64	1160	6 (1)	5 (3)
23	21	Jackson, NC	Cashiers School on NC 107	1160	7 (5)	5 (5)
24	22	Jackson, NC	8.3 mi. N of Cashiers on NC 107	850	–	7 (5)

Table 1. Continued.

No.	Pop.	County, State	Site Description	Elev. (m)	Sample Size: Yellow Birch	Sample Size: Sweet Birch
25	24	Jackson, NC	Woodfin Cascades Overlook on BRP	1400	5 (4)	5 (5)
26	59	McDowell, NC	Milepost 348 on BRP	1370	5 (3)	5 (5)
27	18	Macon, NC	Along trail to Sunset Rock, Highlands	1250	–	10 (0)
28	27	Macon, NC	Scaly Mtn. on NC 106	1040	5 (3)	5 (5)
29	39	Macon, NC	Lake Sequoyah dam, Highlands	1100	–	5 (0)
30	40	Macon, NC	Bridal Veil Falls, Cullasaja Gorge	1040	5 (3)	–
31	41	Macon, NC	Entrance to van Hook Campground, Cullasaja Gorge	980	–	10 (5)
32	42	Macon, NC	Cullasaja Gorge	910	7 (4)	5 (5)
33	44	Macon, NC	US 64 at Gold Mine Rd.	850	7 (4)	9 (6)
34	46	Macon, NC	11.8 mi. N of Franklin on NC 28	640	–	5 (5)
35	51	Macon, NC	Highlands Biological Station	1160	7 (7)	8 (5)
36	29	Swain, NC	Along trail to Gregory Bald, Great Smoky Mtns. National Park	730	13 (0)	8 (0)
37	31	Swain, NC	Along trail to Gregory Bald, Great Smoky Mtns. National Park	1130	–	5 (0)
38	32	Swain, NC	Along trail to Gregory Bald, Great Smoky Mtns. National Park	1280	7 (0)	–
39	33	Swain, NC	Along trail to Gregory Bald, Great Smoky Mtns. National Park	1490	8 (0)	–
40	47	Swain, NC	Nantahala R.	520	13 (10)	10 (10)
41	64	Swain, NC	Newfound Gap, Great Smoky Mtns. National Park	1460	3 (1)	–
42	36	Transylvania, NC	1.3 mi. E of Toxaway Falls on US 64	850	–	5 (5)
43	52	Transylvania, NC	2 mi. N of Rosman on NC 215	730	5 (1)	–
44	55	Transylvania, NC	1.2 mi. E of population 66 on US 276	670	7 (1)	8 (0)

Table 1. Continued.

No.	Pop.	County, State	Site Description	Elev. (m)	Sample Size Yellow Birch	 Sweet Birch
45	66	Transylvania, NC	Coon Tree Picnic Area off US 276	670	4 (4)	–
46	34	Watauga, NC	0.6 mi. NE of Julian Price Mem. Park, BRP	1160	10 (5)	5 (5)
47	58	Yancey, NC	Milepost 354 on BRP	1580	5 (5)	–
48	8	Oconee, SC	1.2 mi. from GA/SC border on SC 28	490	–	5 (0)
49	60	Sevier, TN	Along US 441 in Great Smoky Mtns. National Park	460	5 (5)	5 (5)
50	61	Sevier, TN	5.8 mi. E of population 60 on US 441	980	–	5 (5)
51	62	Sevier, TN	1.2 mi. E of population 61 on US 441	1100	6 (6)	6 (6)
52	63	Sevier, TN	2.1 mi. E of population 62 on US 441	1280	7 (7)	–

RESULTS

The two birch species differed significantly ($P < .01$ of equal species averages) in all but two of the characters used in this study. Blade width differed between the two taxa at a level of significance of .02. The two birches did not differ in their tendency toward cordiform samaras.

There were significant differences in the amount of variation in some characters between the two species. This was determined by calculating a folded F statistic under the assumption of equal variances (SAS Institute Inc., 1985b). Twenty-six characters (21 of them reproductive characters) had significantly different species variances, with yellow birch always having the greater variance. Additionally, only three sweet birches were ciliate-bracted and none were pubescent-bracted, whereas yellow birch bracts averaged 30.2 cilia on a side and were on average moderately pubescent.

Most characters differed significantly among conspecific populations as determined by one-way analysis of variance. For yellow birch, in only five characters was none of the variation attributable to population differences. In sweet birch, no population effect was evident for eight characters. Nine of the 44 characters manifested a contrasting variation pattern in the two taxa; that is, some of the variation was partitioned among populations in one but not the other taxon.

Fifty-five percent of the characters were significantly correlated with elevation in sweet birch and 64% in yellow birch ($P < .05$). All leaf size characters and most bract size characters were negatively correlated with elevation in both species. In yellow birch the fruits tended to be smaller at higher elevations. In sweet birch the samara body or seed tended to decrease in size as well, but samara size was not correlated with altitude. One might have expected, then, wider wings at higher altitudes or possibly a more cordiform samara. However, there was no evidence of a trend in either character.

In general, the two birches exhibited similar trends; there were some differences. Sweet birch serrations become finer at higher elevations and their bracts become more cruciform. The shorter sweet birch bracts at higher altitudes are due to shorter central lobes, whereas in yellow birch, shorter bract bases and central lobes contribute almost equally to reduce bract length. The samara wings of yellow birch are narrower at higher altitudes and the samara body more ovate.

In order to relate elevation to birch morphology, the eleven measured leaf characters for each population were subjected to a principal component analysis utilizing a correlation matrix for each species. No ratios were used in any principal component analysis. The principal component procedure has the effect of summarizing and reducing the variation of many variables into fewer synthetic variables called principal components. By condensing the variation into fewer variables, detection of factors correlated with the major aspects of sample variation is facilitated. In practice, only the first three principal components are considered biologically relevant. For sweet birch, 49% of the variation in the eleven leaf characters was explained by the first principal component (PRIN1). For yellow birch, 54% of the variation was explained by PRIN1. Figure 1 shows the PRIN1 values for each population plotted against elevation. Both plots depict linear relationships significant at $P \leq .0005$.

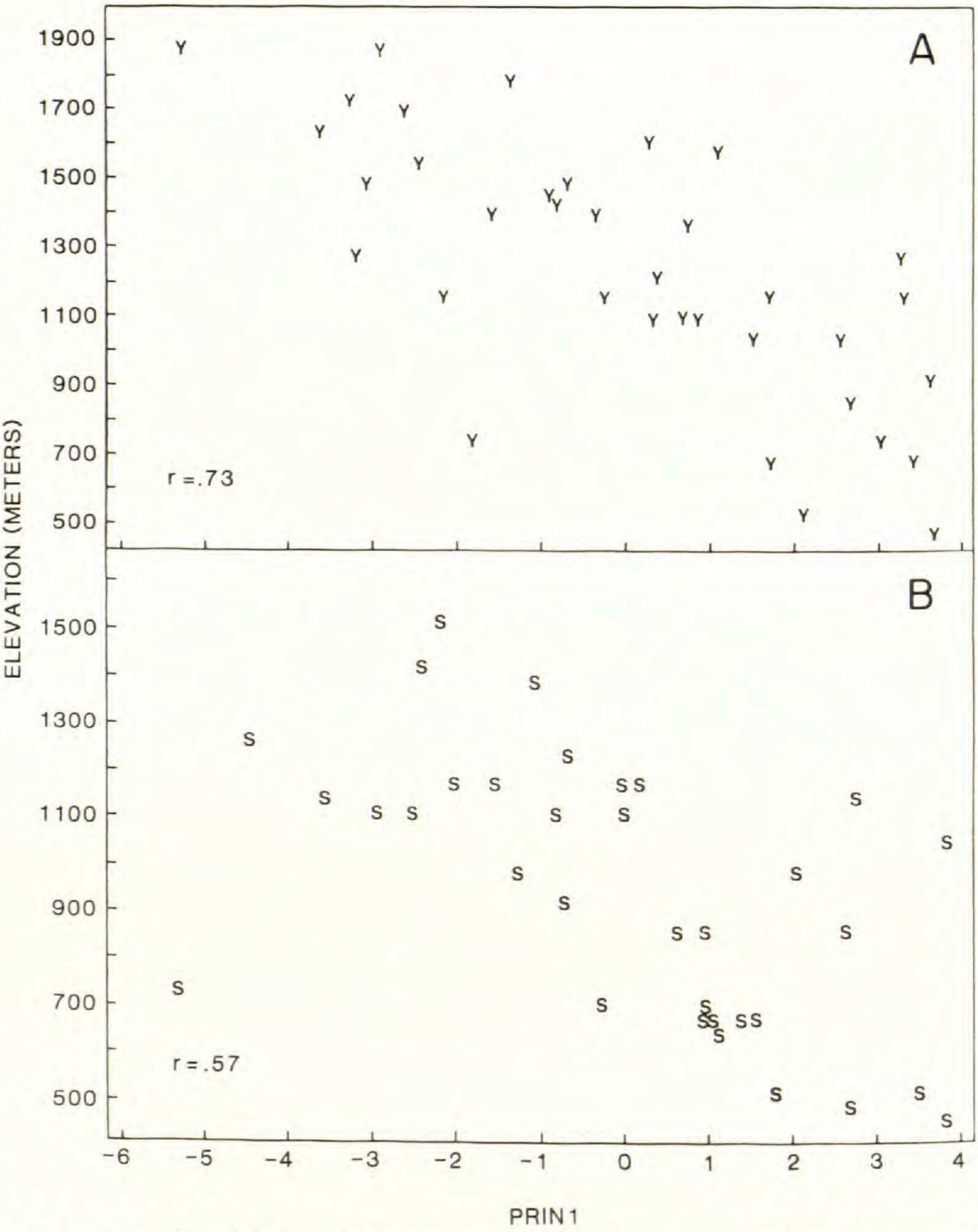

Figure 1. Relationships between population position on the first principal component (PRIN1) and elevation. **A.** For 36 populations of *Betula alleghaniensis*. **B.** For 34 populations of *B. lenta*.

When fruit and bract measurements were also used in the principal component analysis, and the PRIN1 values subsequently plotted against elevation, stronger linear relationships were discerned for each taxon. The sweet birch correlation coefficient (*r*) increased from .57 to .69; the yellow birch *r* value increased from

.73 to .82. Since 13 sweet birch populations and 15 yellow birch populations lacked a complete set of fruit and bract measurements, these results are not graphically illustrated here.

Although the relationship of elevation with birch morphology is predominantly linear, a few quadratic effects were associated with yellow birch fruit and bract characters. The quadratic effects on samara width, bract cruciformity, relative bract central lobe length, and wing width were due to these characters reaching their maximum values in populations between 900 m and 1200 m rather than in populations below 900 m. Populations below 1200 m tended to be more similar to each other in bract base length and samara size than did populations above 1200 m.

DISCUSSION

The results indicate that Britton in 1904 collected yellow birch from one extreme of a clinal pattern of morphological variation. Indeed, he stated that he sampled trees from the upper slopes of Mt. Pisgah, which would put the site above 1500 m. His taxon, *Betula alleghaniensis,* was smaller in stature than *B. lutea,* with bracts shorter than 6 mm and leaves with cordate bases. Our lowest sample average for bract length was 4.3 mm from population 57. Populations 25, 63, and 64 also contained individuals with bract lengths of less than 6.0 mm. In general, high-elevation yellow birches tend to be smaller in habit than their low-elevation counterparts, a condition which is typical of orchard-type vegetation (Braun, 1950). Though Britton characterized his taxon as having a cordate leaf base, the plate of *B. alleghaniensis* in his *North American Trees* (1908) clearly shows cuneate leaf bases. This character is consistent with the data presented here, in that our leaf base character did not vary in a systematic fashion.

Britton (1904) further diagnosed his yellow birch as having bark either yellowish-gray or close and furrowed. We have observed a wide range of variation in the bark of southern Appalachian yellow birch. Many individuals have tight bark tending towards gray or brown. Population 45 is particularly well endowed with this bark variant. Fassett (1932) described a dark, tight-barked variant from Wisconsin as forma *fallax*; the range of this form is, then, extended from Wisconsin, Michigan, Indiana, and Ohio (Clausen, 1973) south to include North Carolina. On the other hand, lighter

Table 2. Species means for ten *Betula alleghaniensis* morphological characters as calculated by four different sources. All values are in millimeters.

Character	Range Wide[a]	Western Great Lakes[b]	Appalachians[c]	Present Study: Populations Below 1200 m	Present Study: Populations Above 1200 m
Blade length	—	109.5	106.0	109.6	92.6
Blade width	—	63.2	58.2	58.9	50.8
Petiole length	—	16.6	13.9	13.7	10.6
Blade length II	—	46.7	43.9	49.4	41.2
Vein pairs	—	14.5	15.2	15.0	14.4
Bract length	8.0	—	9.3	9.5	7.0
Bract base length	5.5	—	6.1	5.6	3.9
Bract width	5.9	—	6.8	7.5	6.2
Seed length	3.2	—	3.5	3.2	2.9
Seed width	1.8	—	1.7	1.7	1.7

[a] Clausen, 1968.
[b] Dancik and Barnes, 1975.
[c] Sharik and Barnes, 1979.

than typical silvery-barked yellow birches, common in New England (Clausen, 1973), were well represented in population 16.

In neither species did we find evidence of the bimodal pattern of distribution with elevation reported by Whittaker (1956). Moreover, his observation that high- rather than low-elevation yellow birch is more similar to the yellow birch of more northerly latitudes is contradicted by our data. Table 2 lists the species means for ten morphological attributes as calculated from four different collections. All but samara body width are negatively correlated with elevation in the southern Appalachians. This finding means that the averages for higher-elevation populations are less than the species average for these nine characters. It is the low-elevation southern Appalachian *B. alleghaniensis* that is more similar to the northern form, at least in its leaf, bract, and fruit morphology.

A number of discrepancies exist between our findings and those of Sharik and Barnes (1979). They found sweet birch samara width and samara body width increased with increasing elevation. We found both characters to vary independently of elevation. Samara length and samara body length varied independently in Sharik and Barnes' study but are negatively correlated here. Whereas we found secondary vein number in yellow birch to decrease at higher altitudes, Sharik and Barnes found it to increase. Sweet birch petiole length was not related to elevation in the earlier study and is negatively correlated in ours. We did not find a significant trend in sweet birch leaf base shape as Sharik and Barnes did. From their complex data set, Sharik and Barnes concluded that trends in morphological variation occurring with changes in elevation do not necessarily occur in a similar manner throughout the Appalachians. Our results support this conclusion.

Some trends were consistent. The two birches are relatively smaller leaved at higher elevations throughout the Appalachians. Sweet birch has relatively smaller teeth at higher altitudes over its entire range. Yellow birch samara wings become narrower with increasing elevation.

In assessing regional morphological variation, we found southern Appalachian levels of variability to approximate or exceed levels elsewhere. For example, the range of population means for yellow birch blade length is 13 mm greater in the southern Appalachians than in the western Great Lakes region (Dancik and Barnes, 1975). Of the eight characters used here that were also used in the western Great Lakes study, five had greater ranges of population means in the present study, even though the present study is smaller both in number of trees and number of populations sampled. The fact that for eighteen characters used in both studies more variation was also found in our regional study than was found by Sharik and Barnes (1979) throughout the Appalachians suggests that elevational amplitude helps maintain variability.

Levels of variability also differ between the species. Our results show that yellow birch is significantly more variable than sweet birch in 28 of the 44 characters analyzed. In no character was sweet birch significantly more variable. Since the comparison is between a hexaploid, yellow birch, and a diploid, sweet birch (Woodworth, 1929), our findings support the long held supposition that polyploids possess greater ecological and genetic amplitude and, therefore, exhibit greater variability than related diploids (Stebbins, 1966; Porter, 1967; Jackson, 1976). There appears to be consistency within the genus in this regard. The tetraploid *Betula pubescens* Ehrh. is reported to be more variable than its nearest diploid relative, *B. pendula* Roth (Gardiner, 1984).

Our results do not support the integrity of Fernald's (1922) long bracted variety of yellow birch, *Betula alleghaniensis* var. *mac-*

rolepis (Fern.) Brayshaw. Variety *macrolepis* was distinguished by its 8 to 13 mm long fruiting bracts. Thirteen of the yellow birch populations we studied include some individuals with average bract lengths less than 8 mm and some with average bract lengths in excess of 8 mm. Because of the gradual nature of the morphological cline in both species and the variability maintained at any given elevation (Figure 1), we agree with Clausen (1973) and Hardin (1971) and find no validity to varietal distinctions in yellow birch.

Clinal patterns of variation have been reported in a number of eastern North American woody species. Kellison (1968) and Mercer (Master's thesis, N.C.S.U., Raleigh, 1969) demonstrated morphological character clines in *Liriodendron tulipifera* L. and *Fagus grandifolia* Ehrh., respectively, from the mountains to the coast of North Carolina. McDougal and Parks (1984) sampled *Quercus rubra* L. over an elevational transect in the southern Appalachians and documented a flavonoid chemical cline in that species. Fryer and Ledig (1972) reported morphological and physiological clines in *Abies balsamea* (L.) Mill. over an elevational transect in the White Mountains of New Hampshire. Relationships with elevation in the White Mountains have also been reported for *Acer saccharum* Marsh. leaf morphology and rates of photosynthesis and respiration (Ledig, 1971; Ledig and Korbobo, 1983).

In Scotland, *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman becomes smaller leaved with increasing altitude. Gardiner (1984) applied the varietal name, *microphylla,* to this small leaved, high-elevation birch and stated that it is apparently "genetically stable." On the high mountain peaks of the northern Appalachians, *Betula cordifolia* Regel is a component of the krummolz (elfinwood) vegetation. The clinal pattern of variation described here appears to be common in the genus. It cannot, however, be stated that it is a general phenomenon in the southern Appalachians. Braun (1950) noted that dwarfing is sometimes conspicuous on the windswept ridge crests of southern Virginia and Tennessee. She observed not only greatly reduced stature, but also reduced leaf size in sweet birch and other species. Mercer (Master's thesis, N.C.S.U., Raleigh, 1969), however, reported that *Fagus grandifolia* was larger leaved at higher elevations in North Carolina. Patterns of variation depend on the racial history of a taxon as well as environmental influence.

Though environment certainly influences phenotypic expression of birch genotypes, it is not unlikely that the observed patterns of variation have genetic components. In another study (unpubl.) sweet and yellow birches grown from seed collected at different elevations in the southern Appalachians were planted outside in Chapel Hill in 1979 and 1980. In April, 1984, bud expansion data were taken on these birches. Our preliminary analyses agree with Clausen (1973) and show that high-elevation birches leaf out later than low-elevation birches and that this trait is genetically controlled. Our observations of flowering phenology in the Chapel Hill plots agree closely with our bud expansion data.

Gene flow via pollen migration, then, may be partially restricted on the southern Appalachian mountain slopes. Genes controlling morphological traits in high-elevation populations at least could differ in their allelic composition from those in low-elevation populations. It is not possible, from our phenological data or from our observations of natural stands, to measure the length of the flowering period in the mountains or the extent of flowering overlap or even synchrony at different elevations on one mountain slope. Such things certainly vary from year to year and slope to slope. However, from our observations of flowering phenology in natural stands, it appears that birches growing below 600 m seldom if ever cross with birches growing above 1500 m. This moderate level of genetic isolation may have allowed sufficient genetic differentiation to bring about the observed pattern of morphological variation.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the financial assistance of the U.S. Forest Service (Southeastern Forest Experiment Station) and grants-in-aid to the first and third authors from the Highlands Biological Station. The authors thank representatives of Blue Ridge Parkway, Nantahala National Forest, Pisgah National Forest, and Great Smoky Mountains National Park for permission to collect plant material. Finally, the authors are indebted to J. R. Massey, R. K. Peet, J. F. Wendel, and two anonymous reviewers for critical reviews of the manuscript.

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